

Herbicide-resistant crops: yield penalties and weed thresholds for oilseed rape (*Brassica napus* L.)

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Summary: Résumé: Zusammenfassung

An experimental procedure was designed to provide a simple model for types of analyses necessary to determine weed density thresholds for advantageous use of crop plants engineered for herbicide resistance. Oilseed rape (*Brassica napus* L., cv. Tower) biotypes resistant (RES) and susceptible (SUS) to atrazine were used as model crop plants, and wild oat (*Avena fatua* L.) was used as the model weed. Along a wild oat density gradient equivalent to 0–128 plants m^{-2} , RES plants consistently experienced biomass and yield reductions of approximately 10–20% compared to SUS plants. When atrazine was applied at 1.5 kg ha^{-1} to control wild oats competing with RES plants, RES biomasses and yields were stabilized at the same level as that where 25–30 wild oats m^{-2} reduce yields of SUS plants. This implies that with wild oat densities of 25–30 plants m^{-2} , it becomes agronomically advantageous to crop with RES plants plus atrazine rather than to crop with higher-yielding SUS plants.

Les cultures résistantes aux herbicides: dépressions de rendement et seuils de nuisibilité chez le colza (Brassica napus)

Afin de déterminer les seuils de densité des mauvaises herbes à partir desquels l'emploi de cultures rendues résistantes aux herbicides devient avantageux, un protocole expérimental

visant à établir un modèle simple a été établi. Des biotypes de colza (*Brassica napus* L., cv. Tower) résistants (RES) ou sensibles (SUS) à l'atrazine ont été utilisés comme modèle de culture, et la folle avoine (*Avena fatua* L.) a été utilisée comme modèle de mauvaise herbe. En présence d'un gradient de folles avoines allant de 0 à 128 plantes m^{-2} , les plantes RES ont constamment subi des réductions de rendement et de biomasse d'environ 10–20% par rapport aux plantes SUS. Quand de l'atrazine était appliquée à une dose de 1,5 kg ha^{-1} à des folles avoines en compétition avec des plantes RES, les biomasses et les rendements des cultures se stabilisaient au niveau de cultures SUS freinées par 25–30 folles avoines m^{-2} . Par conséquent, en présence de densités de folles avoines de 25 à 30 plantes m^{-2} , il devient avantageux de cultiver des plantes RES avec apport d'atrazine plutôt que des plantes SUS à plus haut rendement potentiel.

Herbizidresistente Kulturen: Ernteeinbussen und Schädigungsgrenzen, verursacht durch Unkräuter in Raps (Brassica napus L.)

Es wurde eine Versuchsanlage entwickelt, welche die Erstellung eines einfachen Modells zur analytischen Auswertung von Untersuchungen über die Schädigungsgrenzen von Unkräutern in landwirtschaftlichen Kulturen ermöglicht. Das Verfahren ist speziell auf die Frage ausgerichtet, ob die Verwendung von Sorten, die auf erhöhte Herbizidresistenz gezüchtet worden sind, praktische Vorteile bietet. Als Modelle für die Kulturpflanze wurden zwei Biotypen von Raps (*Brassica napus* L. cv. Tower), ein auf Atrazin resistenter (RES) und ein empfindlicher (SUS) gewählt; Wildhafer (*Avena fatua* L.) diente als Unkrautmodell. Mit zunehmender Unkrautdichte von 0 bis 128 Individuen m^{-2} erlitten die

RES-Pflanzen Ernte- und Biomassereduktionen von 10–20% im Vergleich zu SUS-Pflanzen. Beim Einsatz von 1.5 kg ha^{-1} Atrazin zur Bekämpfung des Wildhafers wurde ein Ertrag an Biomasse und Samen erzielt, der demjenigen von SUS-Pflanzen unter dem Einfluss einer Wildhaferpopulation von 25–30 Individuen m^{-2} entsprach. Daraus folgt, dass bei Dichten von 25–30 Wildhaferpflanzen m^{-2} die Verwendung von RES-Sorten, zusammen mit Atrazin, gesamtwirtschaftlich günstiger ist, als der Anbau ertragreicherer SUS-Sorten.

Introduction

Weed plants that are known to be resistant (RES) to atrazine typically exhibit (temporal) rates of seed germination, and seedling emergence and growth that are lower than those of closely related genotypes which are susceptible (SUS) to atrazine (Maplebeck, Souza Machado & Grodzinski, 1982). Similarly, weedy RES genotypes are both less vigorous and less competitive than SUS genotypes in the absence of atrazine (Conrad & Radosevich, 1979). Such lack of vigour in RES plants is due to a minor modification of chloroplast proteins involved in photosynthesis. This modification, involving the substitution of a single amino acid, not only elicits atrazine resistance, but also retards the flow of electrons during photosynthesis (Arntzen, Pfister & Steinbeck, 1982). Consequently, biomass and seed yields of RES plants also would be expected to be lower than those of SUS plants.

Recently, crop plants have been bred specifically for atrazine resistance and released for commercial production (Beaversdorf, Weiss-Lerman & Erikson, 1980). For the reasons stated in the preceding paragraph, it is reasonable to expect such resistance to impart a yield penalty to the crop. However, there are two reasons why this yield penalty does not necessarily reduce the agronomic value of the RES crop plants. Firstly, if the relevant herbicide has residual activity in soil, any resistant crop that can be grown in that soil has considerable agronomic value. Secondly, the effects of unmanageable weeds on related SUS crop plants may greatly exceed the alleged inherent RES yield penalty. Indeed, there must exist a point (T) on a weed density gradient where the yield of SUS plants equals that of RES plants whose competing weeds were controlled with atrazine. This T value represents the weed density

threshold where it becomes agronomically advantageous to sow lower-yielding RES crops in lieu of higher-yielding SUS cultivars (Fig. 1a).

The research reported here was designed to provide a simple model for types of experiments necessary to determine T values for crops bred or engineered for herbicide resistance in the future. Resistant and susceptible lines of the cultivar, Tower, of oilseed rape were used as the model crop plants, while wild oats were used as the model weed. Wild oats were used because they are susceptible to atrazine and their effects on oilseed rape are well documented (Dew & Keys, 1976; Stephenson, 1982).

Materials and methods

Seventy-five pots, each 20 cm diameter and 25 cm deep, were filled with sterilized loam soil. In each of five sets of 15 pots enough wild oat seeds were sown on 29 August 1984 in order to establish a seedling density gradient of 0, 1, 2, 3 and 4 plants pot^{-1} , corresponding with 0–128 wild oat seedlings m^{-2} . In all of these pots, eight seeds of oilseed rape (cv. Tower) were sown on 4 September 1984; emergent seedlings were thinned to 4 pot^{-1} . In 25 of these pots, only seeds of the susceptible form of Tower were sown, whereas in the remaining 50 pots, only seeds of the resistant form of Tower (currently known as 'Triton') were sown. When wild oats were at the 2–3 leaf stage of development, half of the latter group of 50 pots were sprayed with the equivalent of 1.5 kg ha^{-1} of atrazine. A synopsis of the experimental design is shown in Table 1.

From the time of sowing to the emergence of rape seedlings, pots were arranged randomly on greenhouse benches, where lighting was natural, but night/day temperatures were controlled at 15/25°C. From mid-September onward, however, pots were maintained in an outdoor nursery in Canberra, Australia. Pots were spaced 30 cm from one another, they were watered as needed, and were twice provided with 6 g of slow-release fertilizer (with N, P, and K at 10, 2, and 5%, respectively, along with most other nutrients at lesser concentrations).

Both rape and wild oat plants were harvested on 3 January 1985. Total seed production and above ground dry weights were determined for rape plants, but just dry weights for wild oats. All data were collected on a per pot basis. Analyses of

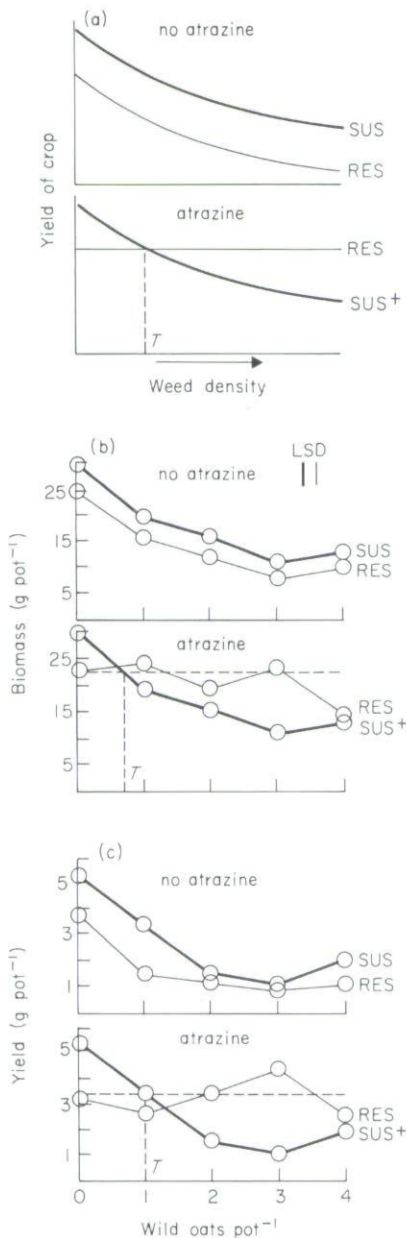


Fig. 1. (a) Idealized yield relationships of atrazine-susceptible (SUS) and atrazine-resistant (RES) crop plants along a weed density gradient in the absence and presence of atrazine. T, the weed density threshold, is that point along the weed density gradient projected from where the yield curve for SUS plants (without atrazine) crosses that for RES plants (with atrazine); (b) biomass and (c) seed yield relationships of SUS and RES oilseed rape plants in the absence and presence of atrazine. Dotted horizontal lines represent average stabilized biomass or seed yield of RES plants after wild oats were controlled with atrazine. SUS⁺ represents superimposed SUS biomass or seed yields (without atrazine). Vertical bars in b represent least significant differences ($p < 0.05$); high variation in c precludes significant differences among means.

variance were performed on dry weight data in order to detect the presence of statistically significant ($P < 0.05$) effects of increasing weed densities on biomasses and yields of oilseed rape plants.

Results and discussion

Biomasses of both RES and SUS plants were reduced similarly (up to 66 and 63%, respectively) and significantly by competition from wild oats along a weed density gradient (Fig. 1b). However, biomasses attained by RES plants were less than those of SUS plants by about 17, 18, 23, 26, and 22% along the gradient of 0, 1, 2, 3, and 4 wild oats pot⁻¹ ($\sim 0, 32, 64, 96$, and 128 plants m⁻²), respectively (Fig. 1b). These results substantiate the well known effects of wild oats on oilseed rape, and they document the alleged 'inherent' reduction in productivity of RES plants.

When the weed density gradient affecting RES plants was controlled with atrazine, weed biomasses were reduced considerably (Table 2). Except at the highest wild oat density, which escaped adequate control, RES biomasses were stabilized at the relatively high level of RES plants

Table 1 Synopsis of experimental design for determination of the weed density threshold where it becomes advantageous to sow atrazine-resistant crop cultivars (RES) in lieu of atrazine-susceptible crop cultivars (SUS)

Genotype	Atrazine applied	Wild oat densities (No. of pots)					Total no. of pots
		0	1	2	3	4	
RES	no	5	5	5	5	5	25
SUS	no	5	5	5	5	5	25
RES	yes	5	5	5	5	5	25

Table 2 Dry weights (g pot⁻¹) of wild oat plants growing with resistant (RES) and susceptible (SUS) biotypes of oilseed rape. Where used, atrazine was applied post-emergence at 1.5 kg ha⁻¹

Associated crop	Atrazine applied	No. wild oat plants pot ⁻¹			
		1	2	3	4
SUS	no	22.5 (4.9)	38.2 (13.7)	38.4 (10.2)	59.0 (9.4)
RES	no	20.6 (5.4)	34.9 (5.9)	43.2 (8.5)	43.6 (10.3)
RES	yes	3.5 (3.5)	6.0 (5.1)	7.0 (4.8)	14.9 (7.1)

Values in parentheses are standard deviations of means

that had grown under weed-free conditions (Fig. 1b). This level of RES biomass accumulation was similar to that produced by SUS plants, which competed with the equivalent of about 0.67–0.75 wild oats per pot or 25–30 plants m^{-2} (Fig. 1b). These results suggest that at the weed density threshold, T, of 25–30 wild oats m^{-2} , it would have been advantageous to have sown the RES form of Tower rather than the inherently higher-yielding SUS form.

Seed yield relationships of both genotypes of oilseed rape (Fig. 1c) along weed density gradients were similar to those of biomass relationships (Fig. 1b). However, the data were more variable, and did not differ significantly along the weed density gradient. Nevertheless, in the absence of atrazine, RES plants yielded less than SUS plants (e.g., 3.9 and 5.4 g pot^{-1} or 1 and 1.4 T ha^{-1} , respectively, with no wild oats). However, when wild oats were controlled, RES yield was stabilized at a relatively high level (3.4 g pot^{-1}); which was equivalent to that of SUS plants affected by 1 wild oat pot^{-1} or 32 wild oats m^{-2} (Fig. 1c). Thus, for seed yield, T equals 32 wild oats m^{-2} ; if wild oat seedling densities equal or exceed this amount then it would have been agronomically advantageous to have sown RES seeds (and apply atrazine) rather than SUS seeds. If wild oat densities are $< 32 m^{-2}$, then higher yields result from sowing the SUS genotype.

Thresholds for yield advantages, however, may be correlated with, but are not equivalent to, thresholds for economic advantages. For calculations of economic T values, monetary credits for crop yield and debits for atrazine use must be calculated. In early 1985, a typical receipt for oilseed rape was \$0.30 kg^{-1} , and the cost of atrazine was \$4.70 kg^{-1} . Application of 1.5 $kg ha^{-1}$ of atrazine has the effect of reducing the value of stabilized RES economic yields by about 2.2%. Such a reduction shifts T to the right, i.e., to approximately the level of 35 wild oats m^{-2} . Thus, if a field can be expected to have wild oat densities $> 35 m^{-2}$, only then would it be economically advantageous to sow that field with the RES form of oilseed rape and apply atrazine to control the weeds. Where wild oats densities are $< 35 m^{-2}$,

then it is more profitable to sow the SUS form of oilseed rape.

Several research laboratories are actively engaged in 'engineering' crop plants that are resistant to a number of herbicides. Should future herbicide-resistant crop genotypes suffer inherent yield penalties, as does atrazine-resistant oilseed rape, then the general type of experiment outlined in this report, validated by field experimentation, is an essential pre-requisite before these crops can be used most profitably.

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